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Original Research Article

Comparative Nest-Site Use and Nest Architecture of *Polistes flavus* and *Vespa orientalis* in District Mardan, Khyber Pakhtunkhwa, Pakistan

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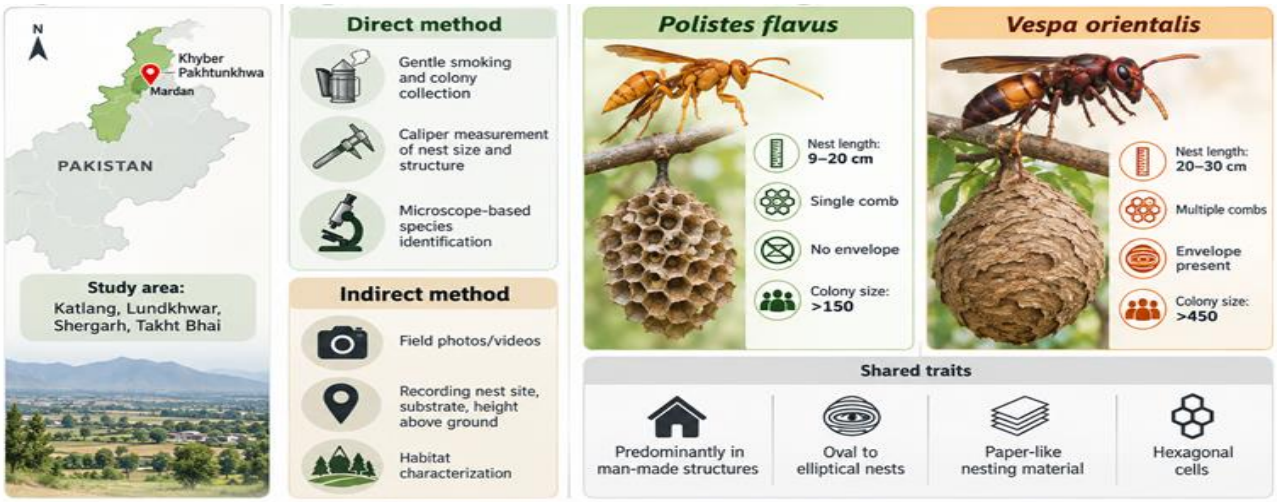
Abstract



Social wasps select nesting environments that must simultaneously support attachment, brood protection, colony growth and access to resources. This study compares documented nest-site use and nest architecture of the paper wasp *Polistes flavus* and the Oriental hornet *Vespa orientalis* in four localities of District Mardan, Khyber Pakhtunkhwa, Pakistan: Lund Khwar, Katlang, Shergarh and Takht Bhai. Field observations combined non-destructive photographic documentation with selective colony collection after gentle smoking, followed by laboratory examination of nests and specimens. The source manuscript reports 16 colonies; however, the supplied row-level field table contains 16 individually documented colonies, eight per species, and quantitative frequencies in this revision are therefore calculated from those 16 records. *Polistes flavus* was recorded primarily on trees (6/8 colonies), with the remaining colonies on buildings (2/8), whereas *Vespa orientalis* occurred mainly in underground cavities (4/8) and buildings (3/8), with one colony on a tree. Correspondingly, six of eight *P. flavus* records were coded as natural sites, while six of eight *V. orientalis* records were coded as man-made. The reported lower-bound colony counts were substantially higher for *V. orientalis* (median 215; range 150-350) than for *P. flavus* (median 45; range 25-90), although these values are approximate because the field log used '+' notation. Nest architecture also differed: *P. flavus* was described as producing open, non-enveloped, usually single-comb nests 9-20 cm long, while *V. orientalis* produced larger, enveloped, multi-comb nests 20-30 cm long. Both species used paper-like material and hexagonal brood cells. The observations support clear species-level differences in documented nest-site use and architecture, However, habitat preference could not be confirmed because the availability of alternative nesting substrates was not assessed. Future studies should evaluate nest-site availability, microclimate, nest dimensions, and seasonal occupancy.

Keywords: Social wasps; Vespidae; *Polistes flavus*; *Vespa orientalis*; nest-site use; nest architecture; anthropogenic habitat; Khyber Pakhtunkhwa.

1. INTRODUCTION

Social wasp nests are extended phenotypes of their colonies: structures built outside the body that affect brood development, worker efficiency, defence and survival. Nest construction therefore represents more than a taxonomic curiosity. The location and architecture of a nest influence exposure to solar radiation, wind, rainfall, predators, competitors and human disturbance, while also constraining how efficiently workers can enter, leave and expand the colony. Classic comparative work on vespid architecture emphasized that variation in comb arrangement, envelope construction and attachment is closely linked to social organization and environmental pressures (Jeanne, 1975; Wenzel, 1998; Batool *et al.,* 2024). More recent research has reinforced the idea that nest design can solve recurring mechanical and thermal problems in different social insect lineages (Smith *et al.,* 2023; Qasim *et al.,* 2025).

Within Vespidae, paper wasps of the genus *Polistes* typically form relatively small colonies and construct exposed paper combs attached to a support by a pedicel. The absence of a complete protective envelope makes the choice of nesting site especially consequential, because shade, shelter and local microclimate can partly substitute for architectural insulation. Experimental and observational work in *Polistes* shows that nest placement can affect thermal conditions and reproductive decisions, and that sheltered sites can produce a brood microclimate that differs from ambient conditions (Jeanne and Morgan, 1992; Kovac *et al.,* 2023; Qasim *et al.,* 2026; Ather at al., 2026). Consequently, a tree branch, roof edge, wall cavity or other support cannot be treated simply as a location label; each represents a distinct combination of attachment stability, thermal exposure and disturbance risk.

Vespine hornets show a different architectural syndrome. *Vespa* colonies often reach larger population sizes and many species build multilayered comb systems surrounded by an envelope. *Vespa orientalis* is broadly distributed from North Africa and the Mediterranean through the Middle East into parts of western and southern Asia, and it also has demonstrated potential for range expansion outside its native distribution (Smith-Pardo *et al.,* 2024). Its nesting biology includes concealed or cavity-associated sites as well as nests associated with human structures (Archer, 1998; Qasim *et al.,* 2026c). For large colonies, enclosed cavities and an external nest envelope may jointly reduce environmental exposure, although direct functional claims require measurements of temperature, humidity, rainfall exposure and colony performance rather than inference from architecture alone.

The ecological importance of social wasps also makes their nesting ecology relevant beyond species description. Wasps can function as predators of arthropods, flower visitors, scavengers and components of food webs, and a growing synthesis literature argues that their ecosystem services have been undervalued relative to more familiar insects (Brock *et al.,* 2021; Qasim *et al.,* 2026b; Ullah *et al.,* 2026). At the same time, colonies established in buildings or other frequently used human spaces can generate conflict because defensive stinging risk increases near active nests. Understanding where different species establish colonies is therefore useful for biodiversity assessment, urban ecology, pest-risk management and conservation of beneficial predatory insects.

1.1 Regional context and study rationale

Pakistan supports a diverse Vespid fauna across climatic and topographic gradients, but detailed quantitative studies of species-specific nest-site use remain limited for many regions. Work from Khyber Pakhtunkhwa has documented *Polistes flavus* nests and described their architecture and nesting behavior, including use of vegetation and paper-like nest material (Perveen and Shah, 2013; Shah *et al.,* 2013). Taxonomic surveys in northern Pakistan further confirm that *Polistes* is an important component of the regional social-wasp fauna (Khan *et al.,* 2018). These studies provide a valuable baseline, yet local nesting patterns may vary among districts because tree cover, building density, farming practices, microclimate and nesting cavities differ at relatively small spatial scales.

District Mardan is suitable for a local comparison because the landscape contains both built environments and natural or semi-natural substrates within short geographic distances. The original field study sampled Lund Khwar, Katlang, Shergarh and Takht Bhai. These localities provide opportunities to encounter colonies on buildings, trees and in underground spaces. A direct comparison of *P. flavus* and *V. orientalis* within the same district can therefore reveal whether two social wasps occupying the same broader environment nevertheless use contrasting nesting substrates and construct structurally different nests.

The primary objective was to compare documented nest-site use and nest architecture of *P. flavus* and *V. orientalis* in District Mardan. Specifically, the study aimed to: (i) summarize the occurrence of colonies among tree, building and underground sites; (ii) compare the natural versus man-made site classifications recorded in the field log; (iii) describe differences in reported colony size, nest length, envelope formation and number of combs.

2. MATERIALS AND METHODS

2.1 Study area

The field study was conducted from March to September 2024 in District Mardan, Khyber Pakhtunkhwa, Pakistan, with sampling in four named localities: Lund Khwar, Katlang, Shergarh and Takht Bhai. The district includes hilly terrain toward the north-east and more extensive plains toward the south and

west. This landscape mosaic contains agricultural areas, settlements, trees, walls, buildings and soil cavities that can provide nesting opportunities for social wasps. Exact geographic coordinates, elevation, vegetation cover and standardized habitat-area measurements were not included in the supplied source file; they should be added in a future submission if the original field notebooks or GPS records are available.

2.2 Field survey design and colony detection

Colony searches were conducted within the four localities using direct observation of potential nesting substrates and visual confirmation of wasp activity. The study indicates that nests were encountered on buildings, trees and in underground spaces. Photographs and videos were used to record nests in situ before or without removal. Recorded attributes included site of colony, broad location class (natural or man-made), observation date and time, an approximate colony-member count, species identity and the number of collected specimens.

2.3 Direct and indirect observation procedures

Two complementary approaches were used. Under the direct method, selected active colonies were subdued by gentle smoking and collected with hand nets. Nests and specimens were then transported for laboratory examination. The caliper was used for nest measurements and a microscope for specimen examination and morphometric work. Naphthalene balls were used for temporary protection of preserved insect material from secondary infestation. Under the indirect method, colonies were documented in place with a high-definition camera, allowing nest location, substrate and approximate height above ground to be recorded without disturbing the colony.

2.4 Species nest characterization

Nest architecture was summarized from measurements and descriptive observations was performed. The reported *P. flavus* nests were 9-20 cm long, lacked an enclosing envelope and were described as single-comb structures. *V. orientalis* nests were reported as 20-30 cm long, enveloped and multi-combed. Both taxa were described as using paper-like material and producing hexagonal cells. These features are treated as study-level observations; the source file does not supply an individual nest-length value for every colony, so no variance, confidence interval or inferential test is calculated for nest length.

2.5 Data integrity, analytical scope and descriptive statistics

The 16 colonies were examined, but the supplied field table contains 16 row-level records with enough information to identify species and nesting site. The quantitative analysis therefore uses n = 16 documented colonies (eight *P. flavus* and eight *V. orientalis*). Colony-member values in the field log are written as lower bounds (for example, 40+ or 250+). For transparency, the numeric component was used only as a minimum reported count. Medians, means and ranges calculated from these values describe the lower-bound numbers written in the field table, not exact colony sizes. Site frequencies were tabulated for Tree, Building and Underground categories and for the Natural versus Man-made coding included in the original dataset. Because sample size is small, sampling effort is unknown and substrate availability was not measured, analyses are descriptive; no chi-square test, logistic model or formal habitat-selection statistic is presented.

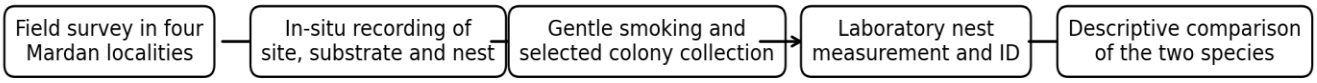


Figure 1: Study workflow reconstructed from the procedures described in the source manuscript. Quantitative summaries in this revision are restricted to the 16 colonies represented by row-level records

3. RESULTS

3.1 Documented colony records

Sixteen colonies in the supplied field table could be linked to a species and a nesting-site record. The dataset was balanced by species (eight *P. flavus* and eight *V. orientalis*) and by locality, with four documented colonies from each of Lund Khwar, Katlang, Shergarh and Takht Bhai. Observation dates ranged from March to August 2024. Table 1 reproduces the analyzable field records in a standardized format.

Table 1: Standardized row-level colony records available in the source dataset. *Colony counts were recorded with '+' notation and therefore represent reported lower bounds rather than exact censuses

Locality	Site	Date	Time	Location class	Colony count*	Species	Specimens
Lund Khwar	Tree	12 Mar 2024	16:00	Natural	40+	*P. flavus*	2
Lund Khwar	Building	20 Mar 2024	13:00	Man-made	150+	*V. orientalis*	3
Lund Khwar	Building	05 May 2024	09:00	Man-made	60+	*P. flavus*	2
Lund Khwar	Underground	10 May 2024	08:00	Natural	350+	*V. orientalis*	2
Katlang	Underground	12 Jun 2024	11:00	Man-made	200+	*V. orientalis*	1
Katlang	Tree	13 Jun 2024	08:00	Natural	50+	*P. flavus*	2
Katlang	Building	18 Jul 2024	14:00	Man-made	30+	*P. flavus*	2
Katlang	Underground	22 Jul 2024	15:00	Man-made	250+	*V. orientalis*	2

Locality	Site	Date	Time	Location class	Colony count*	Species	Specimens
Shergarh	Tree	22 Jul 2024	09:00	Natural	35+	*P. flavus*	3
Shergarh	Tree	25 Jul 2024	14:00	Natural	25+	*P. flavus*	1
Shergarh	Tree	01 Aug 2024	10:00	Natural	230+	*V. orientalis*	2
Shergarh	Building	05 Aug 2024	09:00	Man-made	170+	*V. orientalis*	2
Takht Bhai	Tree	10 Aug 2024	15:00	Natural	70+	*P. flavus*	3
Takht Bhai	Building	15 Aug 2024	14:00	Man-made	330+	*V. orientalis*	1
Takht Bhai	Underground	18 Aug 2024	15:00	Man-made	180+	*V. orientalis*	0
Takht Bhai	Tree	25 Aug 2024	09:00	Natural	90+	*P. flavus*	4

3.2 Nest-site use

The clearest species contrast in the documented dataset concerned nesting substrate. Six of eight *P. flavus* colonies (75%) were on trees and two (25%) were on buildings; none of the row-level *P. flavus* records was underground. In contrast, four of eight *V. orientalis* colonies (50%) were underground, three (37.5%) were associated with buildings and one (12.5%) was on a tree. Thus, tree-associated nesting dominated the *P. flavus* observations, whereas cavity- or structure-associated sites dominated the *V. orientalis* observations (Figure 2).

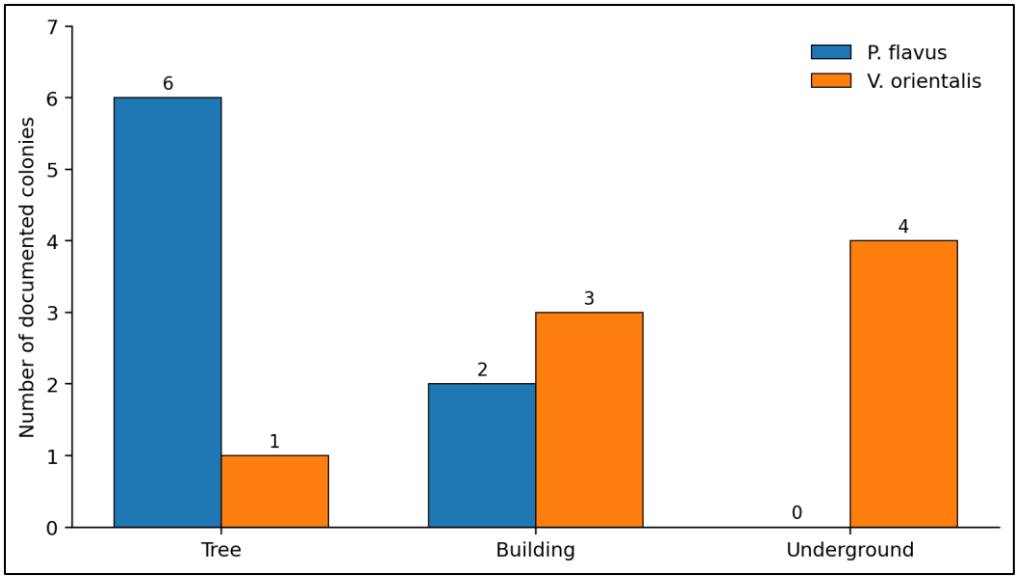


Figure 2: Number of documented colonies by nest-site category. Counts are based on the 16 row-level records supplied for reanalysis (n = 8 per species)

Table 2: Nest-site frequencies and broad location coding among documented colonies

Variable	*P. flavus* (n=8)	*V. orientalis* (n=8)
Tree	6 (75.0%)	1 (12.5%)
Building	2 (25.0%)	3 (37.5%)
Underground	0 (0%)	4 (50.0%)
Natural location code	6 (75.0%)	2 (25.0%)
Man-made location code	2 (25.0%)	6 (75.0%)

The natural/man-made coding showed the same broad contrast: six *P. flavus* records were classified as natural and two as man-made, while six *V. orientalis* records were classified as man-made and two as natural. One *V. orientalis* tree nest was coded natural, whereas several underground nests were coded man-made, indicating that the broad location class and the physical nesting substrate were not identical variables.

3.3 Reported colony size and nest architecture

Minimum reported colony counts differed markedly between the two species. For *P. flavus*, the numeric lower bounds ranged from 25 to 90 individuals, with a median of 45 and mean of 50. For *V. orientalis*, they ranged from 150 to 350, with a median of 215 and mean of 232.5. These summaries are consistent with larger documented colonies of *V. orientalis*, but the '+' notation prevents treatment of the numbers as complete censuses. Figure 3 therefore presents the individual lower-bound values without inferential statistics.

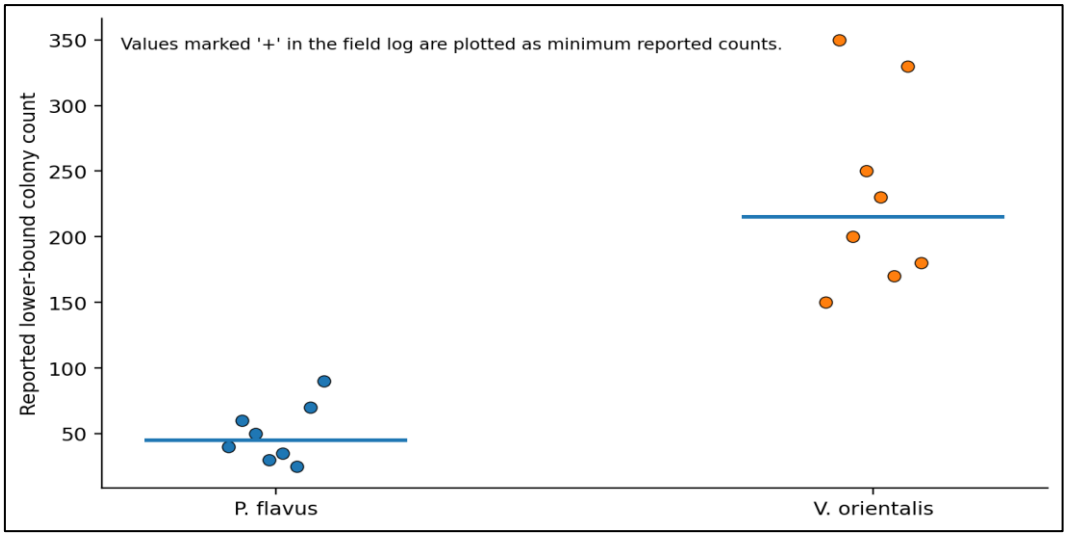


Figure 3: Reported lower-bound colony counts for eight documented colonies of each species. Horizontal lines show medians. Values should not be interpreted as exact colony sizes because the original field log used '+' notation

Table 3: Comparative nest and colony characteristics in the row-level field table

Characteristic	***P. flavus***	***V. orientalis***	**Interpretation in this study**
Reported nest length	9-20 cm	20-30 cm	*V. orientalis* nests described as larger
Envelope	Absent	Present	Open versus enclosed architecture
Number of combs	Usually single comb	Multiple combs	Greater internal subdivision in *V. orientalis*
Cell shape	Hexagonal	Hexagonal	Shared brood-cell geometry
Construction material	Paper-like	Paper-like	Fibrous paper construction reported for both
Dominant documented site	Tree (6/8)	Underground (4/8)	Different observed substrate use
Median lower-bound colony count	45	215	Approximate, not exact census

3.4 Field photographs and qualitative observations

The photographic material embedded provides qualitative context for the field observations. The images show an Oriental hornet foraging on food material, a dense exposed *P. flavus* colony on a tree-supported paper comb, and a *P. flavus* individual on a woody surface associated with the reported nest-construction behavior.

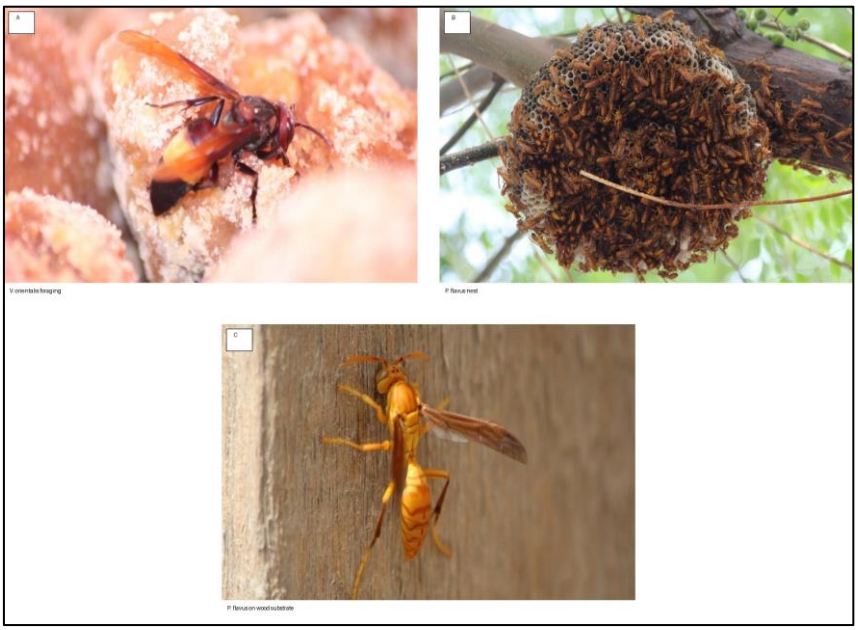


Figure 4: Field photographs supplied with the original manuscript: (A) *V. orientalis* foraging; (B) *P. flavus* nest on a woody support; (C) *P. flavus* on a wood substrate. The panel labels follow the identifications/captions provided in the source file

Taken together, the row-level frequencies, lower-bound colony counts and architectural descriptions indicate a coherent contrast between the two taxa within the documented sample. *P. flavus* was represented mainly by tree-associated colonies and smaller open nests, whereas *V. orientalis* was represented mainly by underground or building-associated colonies and larger enclosed nests.

4. DISCUSSION

4.1 Species differences in documented nest-site use

The most important result is not simply that the two wasps built different nests, but that their documented nesting contexts also differed. Three quarters of *P. flavus* records were on trees, whereas half of *V. orientalis* records were underground and another 37.5% were associated with buildings. This pattern is biologically plausible because an open *Polistes* comb and a large vespine colony face different constraint. An exposed comb requires a stable attachment point and benefits from a sheltered micro-site; a much larger colony can exploit enclosed cavities that accommodate nest expansion while reducing external exposure.

The *P. flavus* observations are compatible with earlier work from Pakistan. Perveen and Shah (2013) described *P. flavus* nests in vegetation and documented the basic paper-comb architecture of the species. Shah et al. (2013) also investigated nesting biology and social behavior of *P. flavus* in Mansehra, providing a regional comparison for the present observations. Agreement across studies should not be taken to mean that *P. flavus* is restricted to vegetation: two colonies in the Mardan records occurred on buildings, and paper wasps in general often exploit human structures when they provide roof edges, cavities, eaves or other protected attachment sites.

The *V. orientalis* pattern is also consistent with a species capable of using concealed nesting spaces. Archer (1998) summarized nesting biology across the Oriental hornet's range, and more recent work continues to treat the species as a flexible, ecologically important hornet with substantial geographic breadth (Smith-Pardo *et al.,* 2024). Underground cavities and spaces within or around buildings can offer a large internal volume and protection from direct rainfall and wind. Such environments may also reduce the need for the nest envelope to perform all protective functions by itself.

4.2 Architectural differences and colony organization

The reported structural contrast between open single-comb *P. flavus* nests and enveloped multi-comb *V. orientalis* nests is consistent with broad differences between polistine paper wasps and vespine hornets. Nest architecture can be considered a coordinated solution to problems of brood placement, abundance, mechanical support, defence and environmental buffering (Jeanne, 1975; Wenzel, 1998). As colonies increase in population, additional comb area and layered construction permit more brood cells to be packed into a limited three-dimensional space. An envelope can further separate the internal comb system from the external environment.

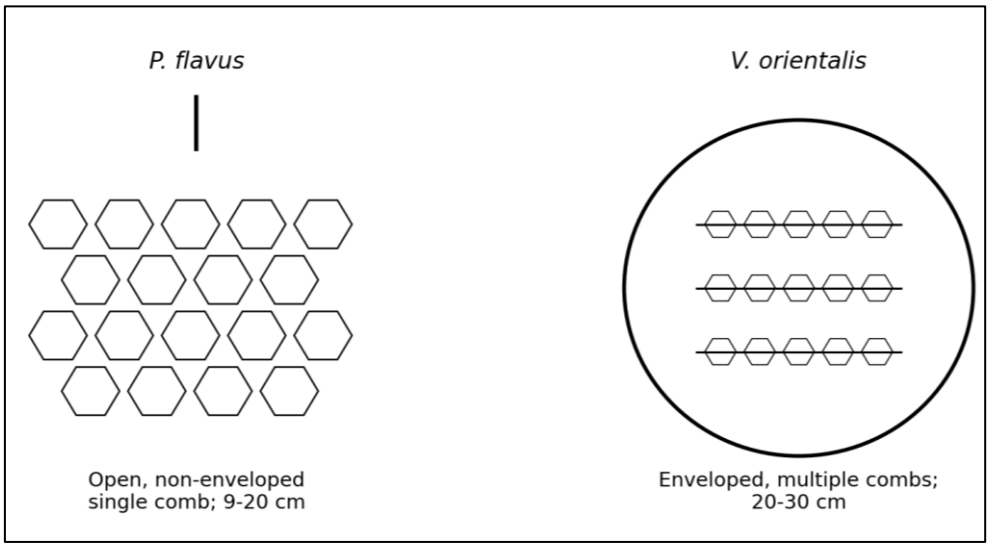


Figure 5: Schematic comparison of nest architecture reported in the study. The diagram is conceptual and not to scale

The shared use of hexagonal cells is also noteworthy. Hexagonal packing is an efficient way to partition a surface into repeated units with shared walls, and comparative work across social wasps and honey bees shows that different lineages can converge on related geometric solutions to nest-building constraints (Smith *et al.,* 2023). In the present study, however, cell shape was recorded qualitatively. Future work could measure cell diameter, wall thickness, comb area and the proportion of cells occupied by brood. Such measurements would convert a simple visual comparison into a quantitative analysis of construction investment.

Paper-like material was reported for both species, but visual similarity does not establish identical material composition. Bağrıaçık (2011) showed that *V. orientalis* nest paper can be characterized in terms of fibre composition and physical properties. Species may differ in the plant fibres, weathered wood, soil particles and salivary components incorporated into their nests. Direct material analysis in Mardan - for example microscopy, fibre identification, mass-per-area measurements and water-absorption tests would allow the study to test whether structural differences arise only from nest geometry or also from construction materials.

4.3 Thermal environment and microclimate as testable mechanisms

One likely reason nest placement matter is microclimate. Social-wasp brood develops within a temperature range that can be influenced by solar exposure, air movement, substrate temperature and the heat produced by adults. In *Polistes* dominula, nest temperature and local microclimate are closely related, and sheltered nest placement can help colonies maintain brood conditions different from ambient air (Kovac *et al.,* 2023). Although that study concerns another *Polistes* species, it demonstrates the kind of mechanism that should be tested directly rather than assumed from site labels.

Nest orientation can also influence passive heat transfer. Bouchebti et al. (2023) experimentally examined heat diffusion in early Oriental hornet nests and found that the orientation of downward-facing cells can contribute to heat movement within the nest. This finding is relevant to *V. orientalis* because it links architecture to a measurable physical process. It does not, however, mean that the Mardan colonies had a particular thermal advantage; no nest orientation or temperature data were recorded in this study.

Thermal measurements would be especially valuable because the two species differ in architecture. An open *P. flavus* comb may respond rapidly to changes in ambient conditions, while an enveloped *V. orientalis* nest in a cavity could experience stronger buffering. Yet it is possible that behavior, worker density or site choice compensates for architectural exposure. Only simultaneous measurement of nest design, colony size and microclimate can determine which mechanism dominates under local conditions.

5. Limitations

The study has important limitations: several potentially important nest, habitat, and microclimatic variables were not recorded at the individual-colony level, limiting the analysis to descriptive comparisons, and sampling was restricted to a single field season, limiting conclusions about long-term or seasonal nesting patterns.

6. Consequence for interpretation

These limitations do not invalidate the field observations, but they change the appropriate conclusion. The strongest supported statement is that the documented *P. flavus* and *V. orientalis* colonies differed in the sites where they were encountered and in reported nest architecture. Claims about true habitat preference, environmental causation, microclimatic advantage or district-wide abundance require additional data. Maintaining that distinction strengthens rather than weakens the paper because it aligns the conclusions with the actual evidence.

7. CONCLUSIONS

The revised evidence from District Mardan indicates a clear difference in documented nest-site use between *P. flavus* and *V. orientalis*. Among the 16 row-level colony records available for reanalysis, *P. flavus* occurred mainly on trees, whereas *V. orientalis* occurred mainly in underground spaces and buildings. The field log also shows substantially larger minimum reported colony counts for *V. orientalis*. Architectural descriptions reinforce this contrast: *P. flavus* was characterized by smaller, open, non-enveloped, usually single-comb nests, whereas *V. orientalis* was characterized by larger, enveloped, multi-comb nests. Both species were described as constructing paper-like nests with hexagonal brood cells. These observations are consistent with broader knowledge of polistine and vespine nesting biology and with regional reports of *P. flavus*. They also generate testable hypotheses about shelter, microclimate, colony size and use of anthropogenic structures. The present dataset, however, cannot demonstrate habitat preference because availability of nesting substrates and standardized survey effort were not measured. The most scientifically defensible interpretation is therefore one of contrasting observed nest-site use rather than proven preference.

Declarations

Ethics statement. Any local permissions required for insect collection or access to private property should be confirmed and reported by the authors before submission.

Data availability. The descriptive analysis in this revision is based on the row-level field table contained in the supplied manuscript. Original photographs and any additional field notebooks should be retained by the authors and made available according to the policy of the target journal.

Conflict of interest. The authors should insert an accurate conflict-of-interest declaration appropriate to the target journal.

Funding and author contributions. To be completed by the authors according to the actual funding sources and individual contributions.

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